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The interspecific growth-mortality trade-off is not a general framework for tropical forest community structure

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50   Resource allocation within trees is a zero-sum game. Unavoidable trade-offs dictate that allocation

51   to growth-promoting functions curtail other functions, generating a gradient of investment in

52   growth versus survival along which tree species align, known as the interspecific growth-mortality

53   trade-off. This paradigm is widely accepted, but not well established. Using demographic data for

54   1111 tree species across ten tropical forests, we tested the generality of the growth-mortality

55   trade-off and evaluated its underlying drivers using two species-specific parameters describing

56   resource-allocation strategies: tolerance of resource limitation and responsiveness of allocation to

57   resource access. Globally, a canonical growth-mortality trade-off emerged, but only in less-

58   disturbance prone forests, which contained diverse resource allocation strategies, was the trade-off

59   strongly observed. Only half of disturbance-prone forests, which lacked tolerant species, exhibited

60   the trade-off. Supported by a theoretical model, our findings raise questions about whether the

61   growth-mortality trade-off is a universally applicable organizing framework for understanding

62   tropical forest community structure.

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66   A widely accepted pattern of life-history tradeoffs in forests is the interspecific growth-mortality

67   trade-off, which emerges because tree species are arrayed on a continuum of resource allocation

68   strategies spanning species that grow slowly and survive well, to species that grow more quickly,

69   but at the cost of higher mortality[1-8]. Provided that species in a forest community fall along such an

70   axis, the growth-mortality trade-off may equalize species' relative fitness and thereby contribute to

71   diversity maintenance[9-11]. The generality of the growth-mortality trade-off, however, has not been

72   unequivocally established because of the need for large demographic data sets spanning multiple

73   census intervals, diverse tree species, and different forest types. Moreover, exploration of the

74   underlying drivers related to alternative resource allocation strategies has focused on functional

75   traits, which often have poor predictive power and have not always shown the expected

76   relationships[6,12,13].

77   Here, we define alternative resource allocation strategies based on the within-species

78   mortality-growth relationship, which reflects demographically integrated outcomes of allocation in

79   response to variation in resource availability. In the interspecific growth-mortality trade-off,

80   species that grow quickly tend to have higher mortality rates (Figure 1a)[3,14,15], but within species,

81   mortality is usually higher for individuals that grow slowly (Figure 1b)[3,16,17]. The lower mortality of

82   faster growing individuals implies that these trees have greater access to above- and/or

83   belowground resources, allowing more resources to be allocated towards reducing the risk of

84   death. Tolerance of resource limitation has long been viewed as an important dimension of plant

85   ecological strategies[18,19]. The mortality rate when growth falls to zero (the within species

86   mortality-growth intercept; Figure 1b) provides an estimate of tolerance and reflects how well a

87   tree can survive with limited ability to acquire and allocate resources to reducing mortality. The

88   slope of the within species mortality-growth relationship (Figure 1b) quantifies how quickly

89   increases in growth translate into reductions in mortality, which we define as the *responsiveness* of

90   species' allocation to resource access. Access to resources is a function of both the resource

91   availability in the environment and a tree's ability to acquire those resources. Individual trees with

92   ample access to resources generally grow faster, which can further increase their access to

93   resources[20] and thereby reduce the impact of allocation trade-offs on demographic rates[21]. The

94   slope therefore reflects variation in access to resources, as well as how trees resolve trade-offs in

95   allocation to growth versus other functions, including survival and reproduction.

96   The shape of the within-species mortality-growth relationship varies widely among tree

97   species[3,14,15], reflecting diversity in tolerance and responsiveness. Forests differ in their long-term

98   environments (*e.g.*, climate, resource availability, disturbance history), and so should also differ in

99   how the underlying trade-offs related to resource access and allocation affect the favorability of

100   different tolerance-responsiveness strategies. Here, we use data on tree growth and mortality for

101   1111 tree species from ten tropical forests representing disparate biogeographic regions and with

102   varying geology, climate, and disturbance regimes (Supplementary Table 1) to test the pantropical

103   generality of the interspecific growth-mortality trade-off and the allocation strategies hypothesized

104   to underpin it. To evaluate our empirical findings, we developed a theoretical demographic

105   allocation model accounting for resource availability in the environment in order to explore the

106   types of allocation strategies yielding the shapes of the within species mortality-growth

107   relationships seen in the real forests we studied and to identify the scenarios under which the

108   interspecific growth-mortality trade-off arises.

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111   **Results**

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113   ***Generality of the interspecific growth-mortality trade-off***

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115   Tree species varied strongly in the shapes of the within-species relationship between individual

116   mortality and prior growth rate (Figure 2; Supplementary Figure 1), which generally explained

117   mortality better than equivalent models without growth as a predictor (Supplementary Table 2).

118   From these models, tolerance and responsiveness parameters were estimated for each species

119   (Figure 1b), and the tolerance parameter and 95th quantile of growth rate were used to define the

120   interspecific growth-mortality trade-off. At the global scale, the trade-off was observed ($r = 0.44$, p

121   < 0.001) across the 1097 species encompassed by the first three-census interval for each forest

122   (Figure 3). We found evidence for the growth-mortality trade-off in eight of the ten tropical forests

123   examined, but the trade-off varied considerably in strength among these forests (Table 1).

124   Statistically significant correlation coefficients ranged from 0.24 (Pasoh) to 0.56 (Lambir) and were

125   largely consistent within each forest among different census intervals, suggesting that the trade-off

126   emerges from the features of the forest. Six of the eight forests that exhibited the growth-mortality

127   trade-off (BCI, Ituri, Khao Chong, Lambir, Pasoh, and Sinharaja) are less disturbance-prone. The

128   least dynamic of these (Lambir, Pasoh, and Sinharaja) have some of the mildest disturbance

129   regimes, consisting mainly of small-scale gap dynamics, less seasonal climates, and often very dark

130   understories, and also occur on fairly nutrient-depleted soils, whereas BCI, Ituri, and Khao Chong

131   are moderately dynamic, having more seasonal climates with more intense dry seasons and more

132   open canopies, or occuring on more fertile soils. Both forests that did not exhibit the trade-off (HKK

133   and Luquillo) and one of the forests with a weaker correlation (Palanan) are highly dynamic and

134   are regularly disturbed by typhoons, hurricanes, or fire (Table 1, Supplementary Table 1).

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136   ***Variation among forests in resource-allocation strategies***

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138   Ordinated based on species' resource allocation strategy (*i.e.*, tolerance and responsiveness

139   parameter values), forests occupied different regions of the global strategy space (Figure 4a), and

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140   how they grouped with respect to biogeography, geology, climate seasonality, and disturbance was

141   inconsistent. Forests in different biogeographic regions often grouped together: Luquillo (Puerto

142   Rico) grouped with HKK (Thailand), Khao Chong (Thailand) grouped with BCI (Panama), while

143   Ituri-Edoro, Ituri-Lenda (Democratic Republic of Congo), Lambir (Malaysia), and Sinharaja (Sri

144   Lanka) grouped together. The first pair are disturbance-prone, the second have more seasonal

145   rainfall regimes and experience occasional, moderate-intensity disturbance, and the last group

146   represents forests growing on more nutrient-depleted soils with lower intensity, smaller-scale

147   disturbances and ample, year-round rainfall (Supplementary Table 1). While variation in

148   disturbance regime was clearly influential in defining differences among forests in strategy space,

149   not all disturbance-prone forests clustered together. Fushan and Palanan (cyclonic forests) did not

150   cluster with each other, nor with the other two disturbance-prone forests (HKK and Luquillo),

151   which themselves clustered together, despite having dramatically different annual rainfall

152   (Supplementary Table 1), further illustrating that climate regime was not always associated with

153   forest grouping patterns. Although Lambir and Sinharaja grouped together and have significant

154   precipitation year-round, other forests (Pasoh, Palanan) with similar climate regimes did not group

155   with them, while Ituri-Edoro, Ituri-Lenda, with a 3-month dry season, did group with them. Fushan

156   occupied a more isolated region of strategy space, while BCI and Khao Chong, with similar annual

157   rainfall, grouped together. Further plot-specific results describing the importance of legacies of

158   disturbance and soil fertility for determining the distributions of tolerance-responsiveness

159   strategies are presented in Supplementary Appendix 1.

160   We divided the resource allocation strategy space into four categories based on the medians

161   of the tolerance and responsiveness parameters across all species and plots: tolerant –

162   unresponsive, tolerant – responsive, intolerant – unresponsive, and intolerant – responsive, and

163   then categorized species in each forest according to their parameter values (Supplementary Figures

164   2 and 3). These groups do not represent absolute categories, but rather provide an informative

165   way to make relative comparisons of how the frequency of species with different tolerance –

166   responsiveness strategies varies among the forests in our analysis. Six species are shown in Figure

167   2 as examples illustrating variation in these strategies. Light-demanding species (Figure 2a and 2b)

168   were generally intolerant-responsive (*Cecropia insignis*, BCI and *C. schreberiana*, Luquillo; Figure 2a

169   and 2b). Shade tolerant species (Figure 2c-f) generally had lower intercepts than light demanding

170   species, but there was considerable variation in both classes, likely driven by other physiological

171   response traits. For example, two congeneric shade tolerant emergent tree species from Lambir

172   that specialize on more fertile clay (*Drylobalanops lanceolata*; Figure 2c) versus infertile sandy loam

173   (*D. aromatica* Figure 2d) soils were both classified as intolerant-responsive. However, *D. lanceolata*

174   had a higher intercept and steeper slope, consistent with the faster growth and higher mortality

175   typical of species specializing on the more fertile clay at Lambir [22]. An extremely shade tolerant

176   tree species, *Anisophyllea corneri* showed the expected tolerant-unresponsive strategy in Pasoh, as

177   did *Dillenia retusa* at Sinharaja (Figure 2e and 2f).

178   Based on data from the first three-censuses for all plots, forests were significantly

179   associated with particular tolerance and responsiveness strategies, (χ^2 = 612.2, *df* = 30, p < 0.001;

180   Supplementary Table 3). Seven of the eight forests in which the growth-mortality trade-off was

181   found (BCI, Ituri, Khao Chong, Lambir, Palanan, Pasoh, and Sinharaja) had more even

182   representation of species among the four types of strategies, whereas forests in which the trade-off

183   was not found (HKK and Luquillo) had more uneven representation of strategies, as they lacked or

184   had very few species in at least two tolerance-responsiveness categories (Supplementary Table 3).

185   This dichotomy generally corresponded to the rate of stem turnover in the forest (forest

186   dynamism), with the exception of Fushan, which exhibited the trade-off, but was dominated by

187   intolerant-responsive species. Tolerant strategies were notably under-represented in the more

188   disturbance-prone forests (Figure 4b). Intolerant species represented > 80% of the species in

189   Fushan and > 90% in HKK and Luquillo. Indeed, Luquillo, which experiences intense, but

190   infrequent hurricanes, had only five species categorized as tolerant, and HKK, with a strong annual

191   dry season and fire disturbances, had only one tolerant species (Supplementary Table 3). Thus, the

192   range of tolerance-responsiveness strategies that are adaptive in disturbance-prone forests, of

193   which 50% did not exhibit the growth-mortality trade-off, was fundamentally different and much

194   more restricted, compared with less disturbance-prone forests, which always exhibited the trade-

195   off.

196   In the five forests for which the within-species mortality-growth relationships could be fit

197   for the same species in multiple three-census intervals (BCI, HKK, Lambir, Luquillo, and Pasoh),

198   estimates for the tolerance parameter were reasonably consistent across intervals for a species

199   (pairwise correlation coefficient: mean 0.73, range 0.50-0.92; Supplementary Table 4). In contrast,

200   estimates of the responsiveness parameter were less consistent (pairwise correlation coefficient:

201   mean 0.26, range 0.04-0.52; Supplementary Table 4). Reproduction is not explicitly represented in

202   our analyses and should trade-off with allocation to support faster growth and reduced mortality

203   risk[23]. This is consistent with the greater within-species temporal variation in the responsiveness

204   parameter in that diverting resources to reproduction could affect the balance between allocation

205   to growth and survival.

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207   ***Theoretical demographic allocation model***

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209   We developed a theoretical demographic allocation model (Supplementary Appendix 2) to explore

210   how alternative resource allocation strategies shape within species mortality-growth relationships.

211   In our model, tree species differ only in their resource allocation strategy, which is defined by two

212   parameters, δ_{0i} and δ_{si}, describing the proportion of total biomass invested in functions promoting

213   survival as function of the availability of all types of resources (*e.g.*, above and belowground

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214   resources) in an individual tree's environment (ω). The parameter δ_{0i} describes the proportion of

215   biomass invested in survival independent of the environment ($\omega = 0$), and δ_{si},

216   describes how that investment changes as the environment improves ($\omega \rightarrow 1$). We examined the

217   relationships between a tree's environment (ω), probability of dying (p), and diameter growth

218   (dD/dt) using five allocation strategies (colors refer to the different strategies in Figure 5a and 5b;

219   see the figure legend for parameter values): (1) *acquisitive*: no allocation to survival functions

220   (blue), (2) *conservative*: constant allocation to survival (red), (3) *prudent*: decreasing allocation to

221   survival with better environments (gold), (4) *opportunistic*: acquisitive, but with increasing

222   allocation to survival with better environments (purple), and (5) *over-conservative*: some allocation

223   to survival that increases in better environments (green). Regardless of the allocation strategy,

224   trees always grow faster in better environments. However, since biomass allocated to survival does

225   not contribute to growth, the increase in growth depends on allocation, with strategies allocating

226   less to survival growing faster in better environments (Supplementary Figure 4).

227   The different allocation strategies produce variation in the relationship between mortality

228   probability and the environment (Figure 5a), which affects the shapes of the within-species

229   relationships between mortality probability and diameter growth rate (Figure 5b), resembling the

230   empirical relationships (Figure 2). The correspondence between the empirical and theoretical

231   results illustrates that interspecific variation in the shapes of the within species mortality-growth

232   relationship can arise solely due to varying strategies of allocation of resources to survival, in

233   combination with varying resource-availability in the environment. In Figure 5, the acquisitive,

234   conservative, opportunistic, and over-conservative strategies (blue, red, purple, and green,

235   respectively) correspond to most of the empirically observed shapes, whereas the prudent strategy

236   (gold), while present, was rarer (Supplementary Figure 1).

237   The acquisitive (analogous to intolerant-unresponsive) and opportunistic (analogous to

238   intolerant-responsive) strategies represent different strategies for taking advantage of

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239   environmental resources. They both allocate no biomass to survival in the poorest environment,

240   but as the environment improves, the acquisitive species allocates all of the additional resources to

241   growth. When there is no direct survival benefit (*i.e.*, not mediated through allocation) of being in a

242   better environment, then the mortality probability of the acquisitive strategy is always high and

243   invariant with growth rate (unresponsive). In contrast, because the opportunistic strategy

244   allocates more to survival in better environments, its mortality probability starts high, but declines

245   as its growth rate increases (responsive). The acquisitive strategy corresponds to the most extreme

246   light-demanding pioneer species that are fast-growing and short-lived, whereas the opportunistic

247   strategy corresponds to less light-demanding species. Like the acquisitive strategy, the conservative

248   strategy displays no plasticity in allocation, but it allocates the same non-zero amount to survival in

249   all environments (tolerant-unresponsive). As a result, it has much lower mortality probability,

250   even in the poorest environments. A similar pattern is observed in the over-conservative strategy,

251   but the faster-growing trees have lower mortality, as this strategy allocates more to survival as the

252   environment improves (tolerant-responsive). The conservative and over-conservative allocation

253   strategies correspond to more shade-tolerant species. The prudent strategy displays a counter-

254   intuitive increase in mortality of faster-growing trees, and this arises because trees in better

255   environments allocate less to survival, so they grow faster, but at the cost of reduced survival. The

256   prudent strategy corresponds to species that prioritize growth and reaching reproductive size.

257   By varying the two parameters describing the resource allocation strategy, a wide range of

258   shapes of the within-species mortality-growth relationship can be generated (Figure 5c), analogous

259   to those in natural forests (Supplementary Figure 1). The tolerance parameter and 95th quantile of

260   growth rate for each species can be calculated from these simulated within-species mortality-

261   growth curves, and a strong interspecific growth-mortality trade-off is produced (Figure 5d). It is

262   also possible to simulate a forest that is dominated by intolerant strategies, as found in more

263   disturbance-prone forests that we studied. Based on 1000 random simulations each of forests with

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264   a wide range of strategies (the 25 strategies in Figure 5c) and with a narrower range of 25

265   strategies, the correlation for the interspecific growth-mortality trade-off is stronger for the forest

266   with a more even distribution of allocation strategies (Supplementary Figure 7). The maximum

267   correlation coefficient was similar for both simulated forest types, illustrating that despite generally

268   weaker relationships, the trade-off can still arise with a narrow range of strategies, as we found in

269   our empirical analyses.

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272   **Discussion**

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274   Life history tradeoffs, including the interspecific growth-mortality trade-off, have been proposed as

275   an important paradigm for explaining tree species diversity in tropical forests. Our analyses of

276   1111 tree species in ten forests spanning all major tropical regions on Earth showed that the

277   growth-mortality trade-off emerged at the global scale, consistent with the idea that unavoidable

278   evolutionary trade-offs shape adaptive variation in tree life history strategies. However, the

279   growth-mortality trade-off was not observed in every forest. The less dynamic forests exhibited

280   stronger growth-mortality trade-offs, whereas the four more disturbance-prone forests exhibited

281   weaker or no trade-offs. Our findings raise questions about the extent to which the growth-

282   mortality trade-off contributes to diversity maintenance by equalizing fitness and suggest the

283   hypothesis that tropical forests exhibiting a weaker trade-off would require stronger stabilizing or

284   other forms of equalizing coexistence mechanisms to maintain species diversity[9-11,24]. While

285   differences in realized rates of population growth ultimately determine the ability of species to

286   coexist, the growth-mortality trade-off may not be a universally applicable organizing framework

287   for understanding diversity maintenance and community structure in tropical forests.

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288   Our approach of using within-species mortality-growth relationships to estimate tolerance

289   and responsiveness, which have been identified as important dimensions of resource allocation

290   strategy[3,18,19,25], allowed us to explore why some forests exhibited the trade-off whereas others did

291   not. The reasons seem to lie in the diversity of resource allocation strategies, as estimated by the

292   empirical tolerance and responsiveness parameter values, of the species in these forests, and our

293   analyses of a novel theoretical demographic allocation model supported this interpretation. Among

294   forests exhibiting the growth-mortality trade-off, there was more even representation of tolerance-

295   responsiveness strategies among species. In contrast, in the forests with little evidence of the

296   growth-mortality trade-off, tolerant species were uncommon and sometimes altogether absent,

297   resulting in a more restricted range of resource allocation strategies. When the variation in

298   resource allocation strategies is small compared to the variation in resource access and acquisition,

299   then expected trade-offs may not be observed, whereas the converse scenario allows trade-offs like

300   the growth-mortality trade-off to be more visible[21,26,27]. Our empirical findings support this idea, as

301   do our theoretical analyses: trade-offs in resource allocation are built into the strategies that we

302   modeled (via the parameter δ), and hence into every simulated forest, but, keeping the

303   environment constant across simulations, only forests with a wide range of resource allocation

304   strategies strongly express the growth-mortality trade-off. Thus, variation in tree species' resource

305   allocation strategies may not only be an important mechanism giving rise to the growth-mortality

306   trade-off, but may also play a role in species coexistence in tropical forests.

307   The variation in the strength of the growth-mortality trade-off that we found across these

308   forests may be partly due to the extent to which the species in them have been filtered for tolerance

309   versus responsiveness strategies. While biogeographic, evolutionary, and ecological forces

310   determine regional species pools, assembly of tree communities from these pools is shaped by the

311   local environment, and these processes ultimately affect the resource allocation strategies that are

312   locally adaptive[28,29]. Forests in which tolerance strategies were favored were also forests in which a

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313   range of strategies was present, and the trade-off was more strongly observed. In these forests,

314   adaptations to tolerate resource limitation appear to anchor the growth-mortality trade-off and

315   represent the constraint end of a wide range of permissible strategies that are differentially favored

316   at any time point in a shifting mosaic of patches[30]. A forest type with only tolerant species,

317   however, cannot exist, because eventually trees die, and there are patch dynamics[30] that favor

318   responsiveness. However, forests in which tolerance strategies are virtually absent can exist,

319   because axes orthogonal to variation in mortality-growth relationships, such as allocation to

320   reproduction[31,32], may be more important in defining life histories in these forests, where

321   disturbances are large and/or frequent, and early and ample reproduction may be particularly

322   critical to population persistence[19]. In such forests, the growth-mortality trade-off may not

323   observed because a full spectrum of tolerance-responsiveness strategies is not present.

324   Compared to the species-specific responsiveness parameter, estimates of the tolerance

325   parameter were more strongly correlated across census intervals, suggesting that tolerance of

326   resource limitation is a more constrained life-history trait. The greater temporal variation in the

327   responsiveness parameter suggests that it is a comparatively less constrained life history trait in

328   that the consequences for survival of previously growing at a given rate may be more

329   environmentally determined. If so, then this may also explain why the growth-mortality trade-off

330   was not observed in the more disturbance-prone forests, in which strategy variation was more

331   defined by responsiveness. There are likely to be sources of mortality, such as drought, lightening,

332   or other disturbances that cannot be avoided even if a tree has access to ample resources in an

333   environment favorable for growth and/or allocates those resources to reducing the risk of death.

334   Likewise, to the extent that allocation to reproduction diverts resources away from growth and

335   survival functions, it may also influence the within species mortality-growth relationship,

336   potentially generating greater variation through time in a species' responsiveness parameter. Our

337   study focused on juvenile to adult trees, which comprises most of their lifespan, but it would be

338   instructive to evaluate whether the same patterns hold at the seedling stage, which comprises a

339   high mortality gauntlet through which trees must pass.

340   Simulations from our theoretical demographic allocation model showed that in a

341   heterogeneous environment, even if tree species only differ in resource allocation strategies, the

342   growth-mortality trade-off can arise provided there is sufficient variation in strategies. In nature,

343   however, our understanding of resource allocation strategies, their plasticity, and fitness

344   consequences in plants, particularly in longer-lived organisms like trees, is still rudimentary. In

345   part, this is because resource allocation strategies are hard to quantify and so are often inferred

346   from functional trait variation[33-35]. There are several complications of this approach. Traits

347   integrate multiple functions relevant to different vital rates, and due to phenotypic integration,

348   different combinations of trait expressions can yield similar demographic outcomes[36]. Trait

349   expression also changes substantially with the environment and through ontogeny[37,38]. As a result,

350   functional trait variation may not accurately capture resource allocation strategies, nor strongly

351   correlate with whole-plant performance[6,12,13,39]. For these reasons, in this study, we estimated

352   resource allocation strategies based on the tolerance and responsiveness parameters of the within-

353   species mortality-growth relationship. We suggest that our understanding of tree life histories is

354   unlikely to be significantly advanced by further observational studies describing large-scale

355   patterns in trait variation in relation to demography. Future studies should use process models

356   parameterized with empirical data to identify physiological and allocation-based mechanisms

357   leading to tolerance and responsiveness and collect longitudinal data on individual allocation to

358   reproduction in order to integrate the key components of lifetime fitness to better understand tree

359   life history strategies.

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362   **Methods**

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Study sites and data

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366 Data on tree mortality and stem diameter growth were obtained from ten plots in the Center for

367 Tropical Forest Science ForestGEO global network of tropical forest dynamics plots, in which all

368 trees ≥ 1 cm in stem diameter at breast height (*i.e.*, 1.3 m above the ground) are censused for

369 survival and re-measured for diameter every ~5 y (Supplementary Table 1)[40]. Plots with at least

370 three censuses were used so that the mortality probability given prior growth could be estimated

371 for each individual tree, with prior growth being estimated during the time interval spanning the

372 first two censuses and mortality being estimated from the second to third census, for any three

373 consecutive censuses. Several plots had multiple three-census sets, and so we analyzed the

374 relationship between mortality and prior growth for a total of 21 forest plot × census interval

375 combinations, comprising a total of 1111 woody species (*i.e.*, excluding palms) and a stem diameter

376 range of 1 to 201 cm across all species in our dataset. In order to compare plots with only three

377 censuses to those with > 3 censuses, only the first three censuses in a plot were considered for

378 some analyses and figures, comprising 1097 woody species across all plots. All analyses were

379 performed in R statistical software[41].

380

Interspecific growth-mortality trade-off and within-species mortality-growth relationship

382

383 The interspecific growth-mortality trade-off is thought to be a trade-off between the ability to

384 survive when resource availability is low versus to grow quickly when resources are plentiful[6,10,16].

385 We therefore estimated the trade-off as the correlation between species' predicted mortality rate of

386 a 1-cm diameter tree that did not grow in diameter in the previous census interval (i.e., the

387 tolerance parameter in Figure 1b) and the 95th quantile of the distribution of diameter growth

15

388   rates. Because species' mortality and growth rates were not normally distributed, we conducted

389   Pearson correlation tests on log-transformed rates and used the best fit lines from standardized

390   major axis regression[42], as implemented in the *smatr* package[43], to visualize the growth-mortality

391   trade-off.

392   We estimated the tolerance parameter from a model of the within-species mortality-growth

393   relationship that was fit separately for each species with (1) at least 200 individual trees having

394   data on mortality given prior growth and (2) at least 5 trees dying from the second to third census,

395   across three consecutive censuses. Because mortality can be a rare event, an abundance threshold

396   of 200 individuals was used to ensure that the mortality-growth relationship was well estimated.

397   Our goal was to estimate species-specific mortality-growth relationships, rather than forest-wide

398   demography. Therefore, we did not use a hierarchical modeling approach, which would have

399   allowed us to include all species, because parameter estimates for rarer species would shrink

400   towards estimates for species with abundant data[44]. Models were run for each species in each plot

401   × census interval combination separately, because none of our statistical inferences relies on the

402   assumption of independence of a species' responses across different censuses and because we were

403   interested in estimating temporal variation in model parameters that could be linked to temporally

404   varying factors such as climate and mass fruiting events.

405   We estimated the within species mortality-growth relationship using a generalized linear

406   model, as implemented in the *glm* function in R. For any three censuses, the mortality probability

407   (p_{ij}) of tree i of species j during the second to third census interval was assumed to be Bernoulli

408   distributed as, $p_{ij} \sim$ Bernoulli(y_{ij},), where y is one if the tree dies and zero if it remains alive. Using a

409   logit link function, mortality probability was modeled as a function of the log-transformed diameter

410   (D_{ij}) at the start of second census and power-transformed prior growth (τ_{ij}) of the tree's main stem.

411   Transformations were used due to the skewness of the distributions of diameter and prior growth.

412   The power transformation of growth rate has the advantage of retaining in the analysis stems with

16

413   small negative growth rates resulting from slight contractions in diameter related to tree water

414   status or slight errors in diameter measurement, which are frequent among slow-growing trees.

415   Thus, $\tau_{ij} = g_{ij}^{0.45}$ for $g \geq 0$ and $\tau_{ij} = -(-g_{ij})^{0.45}$ for $g < 0$. A power of 0.45 has been found to be most

416   effective at reducing skewness in these tree plot data[45]. Prior growth of each tree i of species j was

417   calculated as the annual diameter increment (g_{ij}), which is the difference in diameters of the tree's

418   main stem at two consecutive censuses divided by the time interval between the censuses. Stems

419   with large positive or negative growth values were excluded because they were likely to be

420   erroneous and bias analyses, using a model based on the standard deviation of re-measured

421   diameters from the 1995 and 2000 censuses at the BCI plot[46]. In addition, any tree in which the

422   second diameter measurement was > 4 standard deviations below the first was excluded. Any

423   growth rate > 75 mm/y was also excluded. Thus, the following generalized linear model with a

424   binomial error distribution was fit for each species using the data meeting the above criteria, for

425   any three consecutive censuses: $\text{logit}(p_{ij}) \sim \beta_0 + \beta_1 \ln(D_{ij}) + \beta_2 \tau_{ij}$.

426   We obtained estimates of the intercept (β_0) and slope (β_2) of the within-species mortality-

427   growth relationship for each species in each plot × census interval combination. Tolerance (β_0) and

428   responsiveness (β_2) parameters vary from $-\infty$ to $+\infty$ on the logit scale. Back-transformed to the

429   probability, the tolerance parameter represents the mortality rate of a tree 1 cm in diameter

430   previously growing at a rate of 0 cm/y, and the responsiveness parameter represents the change in

431   mortality probability with variation in growth rate in the prior census interval. Our biological

432   interpretation of these parameters was described in the Introduction (Figure 1b).

433   We performed model diagnostics using the DHARMa[47] and broom[48] packages, including

434   comparing observed versus expected residuals (Q-Q plots), standardized residuals versus predicted

435   values and versus independent variables (($\ln(D_{ij})$ and τ_{ij}), and tests for outliers and over-dispersion.

436   Overall, diagnostic tests showed good fits of our model to data. We evaluated the goodness of fit of

437   our within-species mortality-growth models relative to a simpler model of mortality as a function of

438   only diameter using model selection based on Akaike's Information Criterion (AIC) and PseudoR^2

439   [49,50] for each plot and census year combination. Differences in AIC and PseudoR^2 showed that

440   improvements in explanatory power were achieved when prior growth rate is added to the model

441   as a predictor of mortality (Supplementary Table 2).

442   Growth rate (cm/y) was calculated as described above for each tree using the first and

443   second censuses of any three-census interval, and the 95th quantile of the growth rate distribution

444   was determined. We chose not to use relative growth rate (RGR) because, although it attempts to

445   account for the effects of size on growth, RGR is itself size-dependent and declines as individuals

446   grow[51], which can be problematic for large trees.

447   We evaluated whether using size-standardized growth and mortality rates for each species

448   would result in better estimation of the growth-mortality trade-off than our approach for

449   quantifying the growth-mortality trade-off. To do this, we fit separate linear and nonlinear models

450   of growth (five models) and mortality (four models) as functions of diameter, chose the most

451   supported model for each species based on the Akaike Information Criterion, and predicted growth

452   and mortality at the 25th and 50th species-specific quantiles of diameter. Our analyses indicated

453   that contrary to improving inferences, predicted growth and mortality at a given diameter

454   produced poor predictions for many species for two reasons. First, the confidence intervals on

455   prediction were quite large, since growth and mortality often do not vary strongly with diameter, as

456   has been previously shown e.g., [52]. Second, given the structural complexity of old-growth tropical

457   forests and the stochasticity of death, there is no common diameter that did not produce biased

458   mortality predictions for some species, making the predictions incomparable across species. When

459   all tree deaths happened to fall above or below the diameter quantile, the mortality prediction at

460   that diameter was near zero, creating a large outlier in the mortality rate. Thus, using predicted

461   growth and mortality at a given diameter would create the appearance of size-standardization, but,

462   instead, introduces undesirable inaccuracies and uncertainties that can be avoided with our

463   approach.

464   We chose not to conduct a phylogenetic comparative analysis because if there is no

465   phylogenetic effect (*i.e.*, when more closely related species are not more similar in trait variation),

466   then incorporating phylogenetic information into analyses may be inappropriate[53-55]. This is

467   especially of concern since our analyses include tree species from across the world's major tropical

468   regions, which are still poorly known from phylogenetic and sometimes even taxonomic

469   perspectives. As a result, phylogenetic topologies could be incorrect and will also have many

470   polytomies, possibly producing artefacts in phylogenetic comparative analyses. We therefore chose

471   to avoid these uncertainties and potential biases.

472

473   ***Variation in resource allocation strategies***

474

475   We used the medians of tolerance and responsiveness across all data sets (*i.e.*, all species, plots, and

476   three census interval combinations) to define four resource allocation strategy groups defined by

477   the within species mortality-growth relationship. Species with tolerance (*i.e.*, intercept of the

478   mortality-growth relationship) less than the median were classified as "tolerant," whereas those

479   with tolerance greater than the median were classified as "intolerant." Since slopes of the

480   mortality-growth relationship were nearly always negative, species with responsiveness less than

481   the median (*i.e.*, steeper negative slope) were classified as "responsive," whereas those with

482   responsiveness greater than the median were classified as "unresponsive" (*i.e.*, slope closer to zero

483   or positive). We performed this classification separately for each forest × census interval

484   combination. It is important to note that these tolerance-responsiveness strategy groups depend

485   upon the particular forests included and do not represent an absolute tolerance-responsiveness

486   spectrum. They are, however, a useful way to compare the frequency of different tolerance-

487   responsiveness strategies across the forests in our data. Variation in tolerance and responsiveness

488   parameters across forests, using estimates from models fit for the first three-census interval for

489   each plot, was also visualized using principal components analysis as implemented in the *prcomp*

490   function in R on the parameter values scaled by subtracting the mean and dividing by the standard

491   deviation across species.

492

493   ***Theoretical demographic allocation model***

494

495   We developed a theoretical demographic allocation model to describe a community of tree species

496   distributed along a continuum of resource allocation strategies that differ in allocation to functions

497   promoting growth and survival. Our hypothesis is that species differ in two dimensions of resource

498   allocation strategy: (1) the minimum amount, regardless of their growing environment, that a tree

499   allocates to survival functions, analogous to the tolerance parameter in our empirical analyses, and

500   (2) how much more or less a tree in an environment with greater resource availability allocates to

501   survival functions, compared to a tree with lower access to resources, analogous to the

502   responsiveness parameter in our empirical analyses. We define parameters describing these

503   dimensions, and simulate the growth and survival with respect to a heterogeneous environment of

504   individuals of tree species that vary only in these two dimensions of their allocation strategies. The

505   model is described in detail and analyzed in Supplementary Appendix 2.

506

507

508   **Author Contributions**

509

510   SER conceived and designed the study, assembled and analyzed the data, and wrote the manuscript.

511   SER, GL, and MD designed and analyzed the theoretical model. RSC, SJD, MD, SMM, and SJW made

20

512   important contributions to the interpretation of results and to writing and revising the manuscript.

513   RSC, SJD, PSA, SB, C-HC-Y, SE, CENE, CF, RBF, CVSG, IAUNG, TH, C-FH, SPH, AI, ARK, YTL, YCL, J-RM,

514   MBM, PO, AS, I-FS, ST, JT, TY, SLY, and JKZ contributed to the acquisition of the data used in the

515   paper and in writing the manuscript. All authors have given final approval to publish this

516   manuscript and agree to be accountable for the aspects of the work that they conducted.

517

518

519   **Data Availability**

520

521   The data supporting the findings of this study will be deposited at

522   https://forestgeo.github.io/fgeo/.

523

524

525   **Code Availability**

526

527   The programming code supporting the findings of this study will be deposited at

528   https://forestgeo.github.io/fgeo/.

529

530

531   **Competing Interests**

532

533   The authors declare no competing interests.

534

535

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687

688   **Figure legends**

689

690   **Figure 1.** Conceptual model of the between (A) and within (B) species relationships between

691   mortality and growth for trees. In (A), species fall along the interspecific growth-mortality trade-off

692   axis, which represents a trade-off between the ability to grow quickly when resources are plentiful

693   versus to survive when resources are scarce. While responses to light have been emphasized in

694   defining the trade-off[3,6], belowground resources also affect tree growth and mortality[5,22], and so we

695   consider resources in more general terms. The trade-off arises because tree species with slow

696   growth and high mortality (upper left corner) are selected against, because this combination of vital

697   rates would not be successful in competition with species that grow faster and/or have lower

698   mortality. While a fast growth-low mortality strategy (bottom right corner) would be successful,

699   physiological and allocation-based constraints impose limits, since allocation to functions that favor

700   fast growth reduce allocation to functions that favor survival[56,57]. How trees resolve such trade-offs

701   in resource allocation is thought to generate the interspecific trade-off. In contrast to the between

702   species relationship, within species, individual mortality probability declines with individual

703   growth rate (B). The shape of the within species mortality-growth relationship reflects both

704   evolutionary and ecological influences and integrates differences among individuals in access to

705   exogenous resources and strategies of allocation of endogenous resources. We use the empirical

706   within species mortality-growth relationship for a tree species to derive proxies for two species-

707   specific dimensions of resource allocation strategy thought to underlie the interspecific growth-

708   mortality trade-off: tolerance of resource limitation and responsiveness of allocation to resource

709   access, where "access" integrates both the availability of resources in the environment and a tree's

710   ability to acquire those resources. We mechanistically model tolerance and responsiveness in a

711   theoretical model (Supplementary Appendix 2), however, these dimensions of allocation strategy

712   are not directly observable in empirical data, and so here we use proxy parameters derived from

713   the within-species mortality-growth relationship. The intercept is the mortality rate when growth

714   falls to zero, which reflects tolerance in that it quantifies how well a tree can survive in

715   environmental conditions that curtail growth, which are generally conditions of resource-

716   limitation. The slope quantifies how quickly increases in growth translate into reductions in

717   mortality, which reflects how access to resources directly affects mortality and, importantly, how it

718   affects mortality as mediated by changes in allocation to functions affecting growth versus survival.

719

720   **Figure 2.** Within-species relationships between individual mortality and prior growth for five

721   exemplar tropical tree species. (A) *Cecropia insignis* (Urticaceae), a pioneer tree species from BCI

722   (intolerant-responsive), (B) *Cecropia schreberiana* (Urticaceae), a pioneer tree species from

723   Luquillo (intolerant-responsive), (C) *Dryobalanops lanceolata* (Dipterocarpaceae), an emergent tree

724   species specializing on more fertile soil from Lambir (intolerant-responsive), (D) *Dryobalanops*

725   *aromatica* (Dipterocarpaceae), an emergent tree species specializing on less fertile soil from Lambir

726   (intolerant, responsive), (E) *Anisophyllea corneri* (Anisophylleaceae), a shade-tolerant subcanopy

727   tree species at Lambir (tolerant-unresponsive) and (F) *Dillenia retusa* (Dilleniaceae), a shade-

728   tolerant canopy tree species at Sinharaja (tolerant-unresponsive). Red lines show the mortality-

729   growth curve predicted from the model fit, with the blue shaded region showing the 95%

730   confidence band, at the species' mean diameter at breast height (DBH). Black circles show the

731   predicted mortality probability for each tree at its observed growth rate and DBH and the symbol

732   size is scaled to DBH. Individuals deviate from the predicted line because their DBHs differ from

733   the mean. Rug plots at the bottom and top of the graph show trees surviving (below) and dying

734   (above) at their observed growth rate. Note the changes in x-axis scales.

735

736   **Figure 3.** The interspecific growth-mortality trade-off for 1097 woody tree species in ten forests.

737   Each point represents the estimated mortality rate at zero growth rate (tolerance parameter) and

738   95th quantile of growth rate for a species, with the first three-census interval represented for each

739   forest, so that species only appears once per forest. The dashed black line is the major axis

740   regression line across all species and represents the growth-mortality trade-off at the global scale

741   for the tropical tree species in our study. Solid colored lines represent the major axis regression

742   line for forests with a statistically significant correlation (Table 1), colored according to the legend.

743

744   **Figure 4.** Variation among forests in tree species' tolerance and responsiveness strategies. (a)

745   Principal components analysis of variation in the parameters of the within-species relationship

746   between mortality and prior growth for ten tropical forests. Ellipses represent 95% confidence

747   intervals, calculated based on the standard error, around the centroid for each forest. Different

748   colors indicate the different forests, as shown in the legend in the figure, with less disturbance-

749   prone forests show in yellow, green, and blue ellipses and circular symbols, and more disturbance

750   prone forests show in pink, red, and brown ellipses and triangular symbols. Since there are only

751   two parameters (intercept: species' tolerance of resource limitation and slope: responsiveness to

752   resources), the two principal components together account for 100% of their variation. So that

753   species only appear once, only the first three censuses in a plot were used in this figure, comprising

754   1097 species across all plots. (b) Representation of the four tolerance and responsiveness

755   mortality-growth strategies in more disturbance-prone (Fushan, HKK, Luquillo, Palanan) versus

756   less disturbance-prone (BCI, Ituri-Edoro, Ituri-Lenda, Khao Chong, Lambir, Pasoh, and Sinharaja)

757   forests for the first census interval for each forest. See Supplementary Table 3 for forest-specific

758   values across different censuses.

759

760   **Figure 5.** Analysis of a theoretical demographic allocation model showing the consequences of

761   variation in resource allocation strategies for the growth-mortality trade-off. In (a) and (b), five

762   strategies of resource allocation to survival functions are modeled (see in-figure legend), resulting
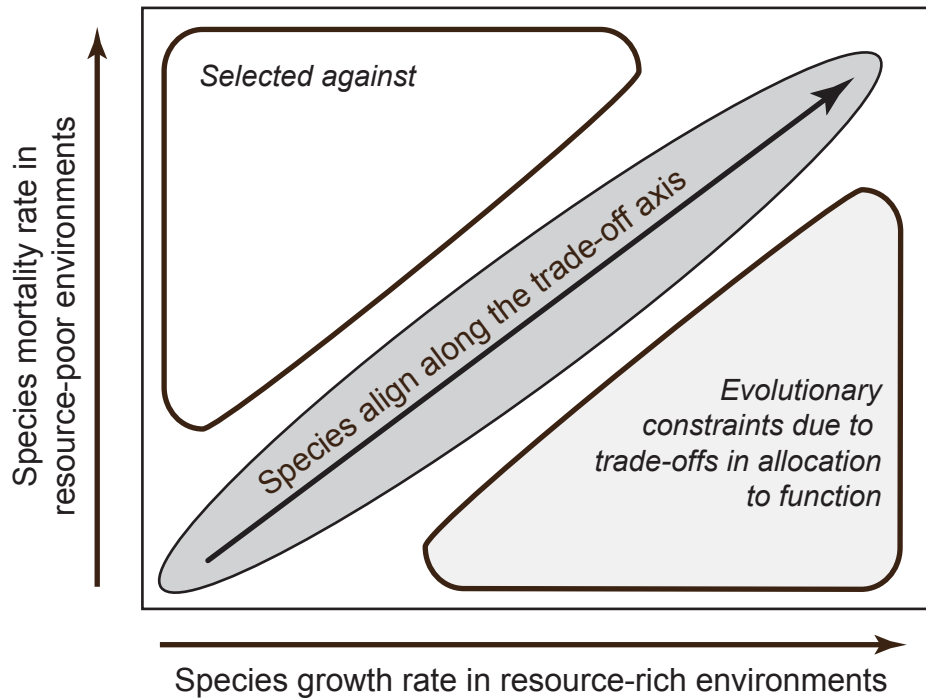
31

763   in variation in the individual-level mortality probability with respect to the resource availability of

764   the environment (a) and with respect to diameter growth rate (b). In (c) the within-species

765   mortality-growth relationships of 25 species representing a wide range of different resource

766   allocation strategies are modeled, and in (d) the corresponding interspecific growth-mortality

767   trade-off for species with these strategies is presented. The growth-mortality trade-off relationship

768   in (d) is statistically significant (Pearson correlation; $r = 0.72$, $p < 0.001$). One species (*i.e.*, strategy)

769   is represented by one line in (a), (b), and (c) and by one point in (d). Resource availability in the

770   environment varies from the lowest ($\omega = 0$) to the highest ($\omega = 1$) availability, and each curve

771   corresponds to one species-level resource allocation strategy defined by δ_{0i} (the proportion of

772   biomass allocated to survival functions in the poorest environment, $\omega = 0$) and δ_{si} (the rate of

773   change of the proportion of biomass allocated to survival functions with respect to the environment

774   (linear with ω)). Note that in (b) and (c), the curves for each species do not extend to all possible

775   growth rates because species that allocate more biomass to survival functions will grow slower

776   than species that allocate less. Thus, the maximum growth rate for each species, corresponding to

777   the right end point of each curve, depends on the maximum amount of resources left over for

778   growth in an ideal environment ($\omega = 1$). See Supplementary Appendix 2 for the detailed model

779   description and analysis.

780

Table 1. Strength of the interspecific growth-mortality trade-off, as measured by the correlations
of species' estimated mortality rate at zero growth rate (*i.e.*, tolerance parameter) with 95th quantile
of growth rate for woody tree species in ten tropical forest dynamics plots. The Pearson correlation
coefficient (*r*) and probability (*p*) for 21 forest plot × census-year combinations is shown, along
with the number of tree species included in each analysis. Plots are grouped according to
disturbance severity, with disturbance associated with fire at HKK and typhoons and hurricanes at
Fushan, Luquillo, and Palanan. The initial census year used to calculate growth and mortality for
successive censuses is listed along with the plot name (Supplementary Table 1). Correlation
statistics in bold are statistically significant at α < 0.05. Since the same species can occur in multiple
censuses in a plot or in multiple plots, the sum of the numbers of species in this table is greater than
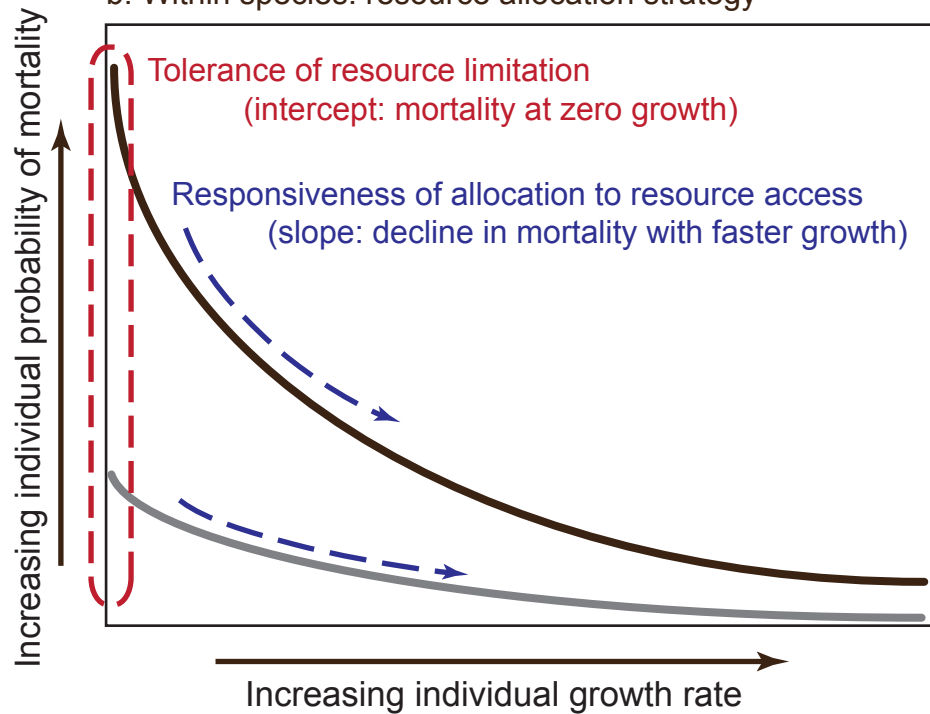the total number of unique species analyzed.

Plot - census year	No. species	*r*	*P*
Less disturbance-prone			
BCI – 1985	101	**0.48**	**< 0.001**
BCI – 1990	98	**0.46**	**< 0.001**
BCI – 1995	91	**0.46**	**< 0.001**
BCI – 2000	90	**0.43**	**< 0.001**
Ituri – Edoro - 1994	54	**0.33**	**0.014**
Ituri – Lenda - 1994	47	**0.41**	**0.004**
Khao Chong - 2000	104	**0.41**	**< 0.001**
Lambir - 1992	359	**0.56**	**< 0.001**
Lambir - 1997	352	**0.54**	**< 0.001**
Pasoh - 1986	312	**0.34**	**< 0.001**
Pasoh - 1990	295	**0.33**	**< 0.001**
Pasoh - 1995	296	**0.29**	**< 0.001**
Pasoh - 2000	281	**0.24**	**< 0.001**
Sinharaja - 1993	85	**0.31**	**0.004**
More disturbance-prone			
Fushan - 2004	39	**0.38**	**0.016**
HKK – 1992	39	0.19	0.255
HKK – 1999	42	0.25	0.105
Luquillo - 1990	31	0.08	0.678
Luquillo - 1995	26	0.12	0.557
Luquillo - 2000	25	0.27	0.176
Palanan - 1998	58	**0.26**	**0.045**

a. Between species: the growth-mortality trade-off

Selected against

Species align along the trade-off axis

Evolutionary constraints due to trade-offs in allocation to function

Species mortality rate in resource-poor environments

Species growth rate in resource-rich environments

b. Within species: resource allocation strategy

Tolerance of resource limitation
(intercept: mortality at zero growth)

Responsiveness of allocation to resource access
(slope: decline in mortality with faster growth)

Increasing individual probability of mortality

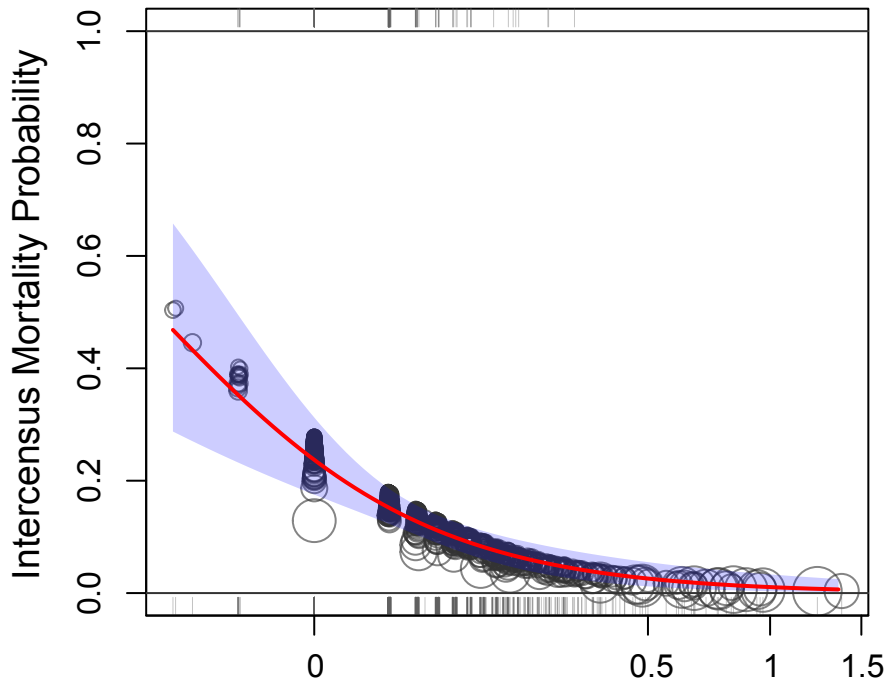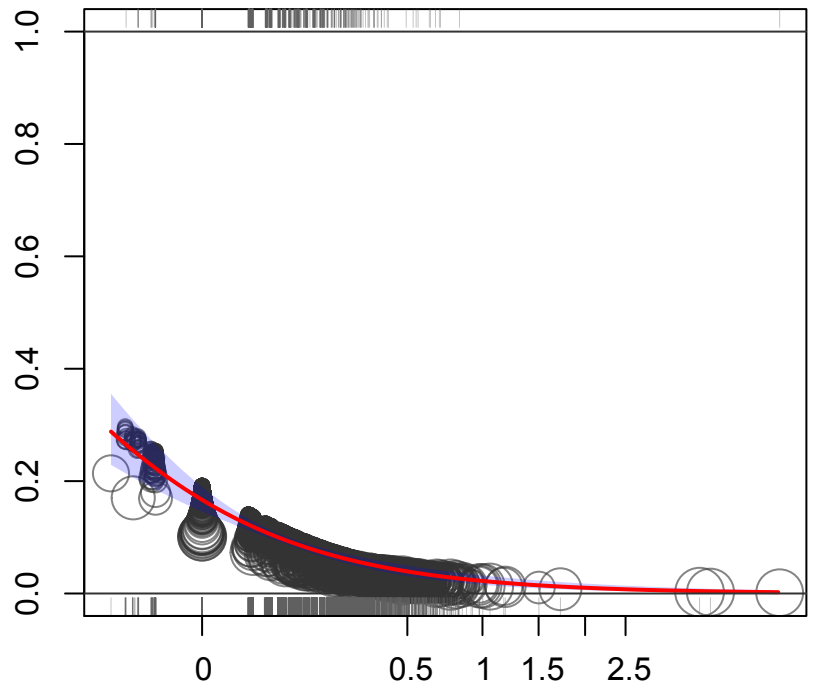Increasing individual growth rate

a. *Cecropia insignis* - BCI
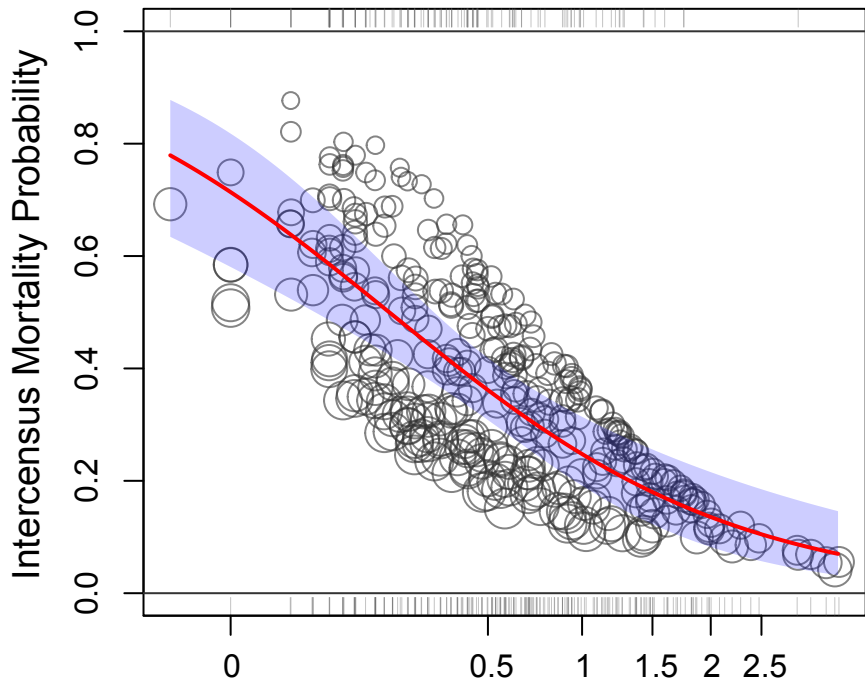
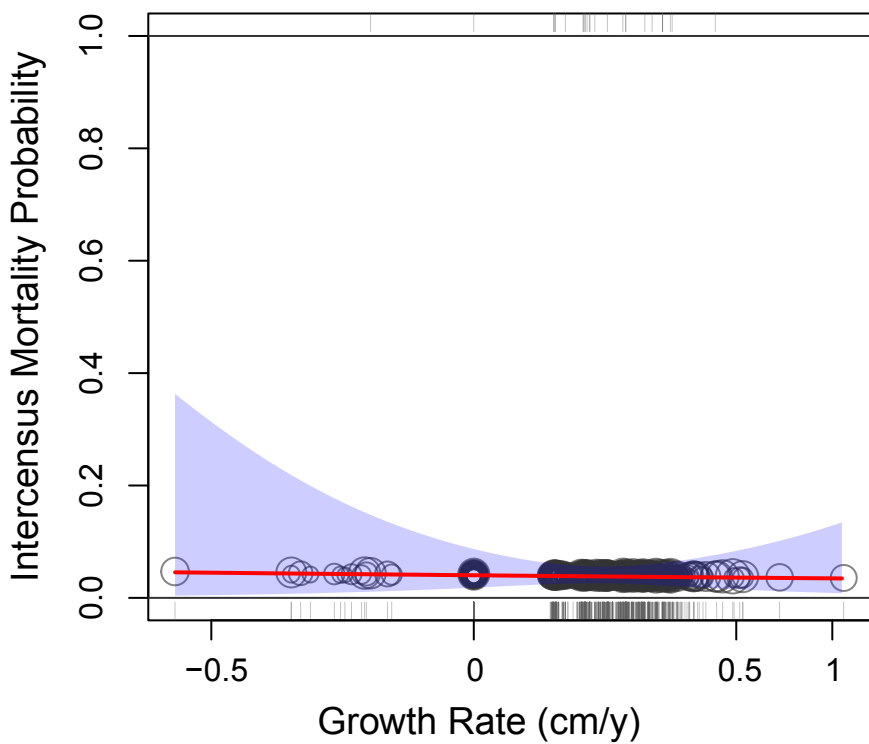b. *Cecropia schreberiana* - Luquillo
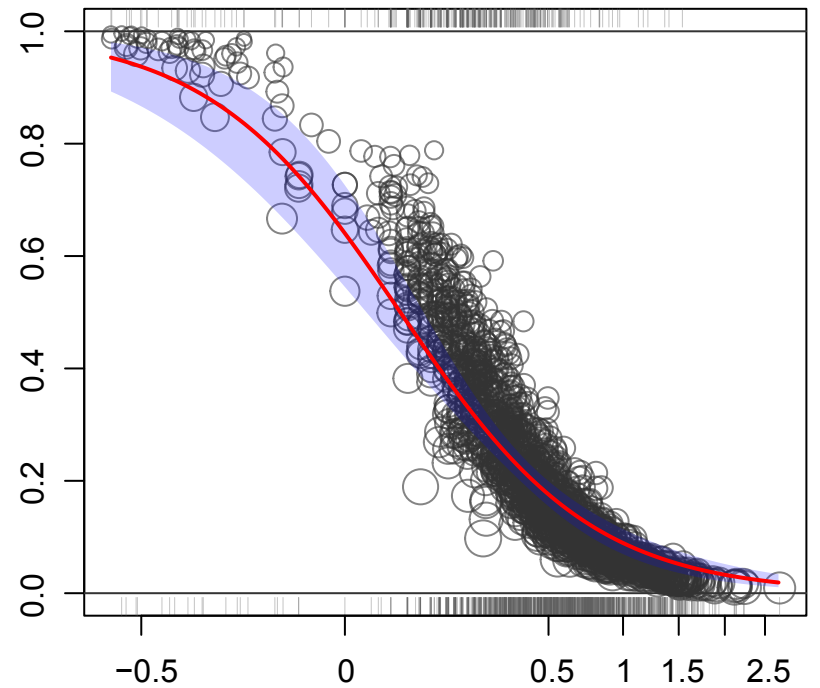
c. *Dryobalanops lanceolata* - Lambir

d. *Dryobalanops aromatica* - Lambir

e. *Anisophyllea corneri* - Pasoh

f. *Dillenia rutusa* - Sinharaja

Intercensus Mortality Probability

Growth Rate (cm/y)

a.

b.